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BIOLOGY AND IMMATURE STAGES OF *CHLOROPS CERTIMUS* AND *EPICHLOROPS EXILIS* (DIPTERA: CHLOROPIDAE), STEM-BORERS OF WETLAND SEDGES

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Abstract.—The life cycles of *Chlorops certimus* and *Epichlorops exilis* are described and illustrated. The adults are found in freshwater marshes where their host plants, species of the sedge genus *Carex,* occur. Eggs are deposited on the sheathing leaves of the host, and the larvae are stem borers. Both species are univoltine, overwintering as nearly mature larvae near the base of the sedge culm. Puparia are formed within the culm, and adults emerge in northeastern Ohio in early to mid-June.

The family Chloropidae, containing about 1,300 species in the world, is one of the more intriguing and colorful members of the cyclorrhaphous Diptera. Some 270 species and 55 genera have been recorded from the Nearctic Region (Sabrosky, 1987). Phylogenetically, the Chloropidae are placed in the superfamily Ephydroidea, a sizeable taxon that includes 9 families of Acalyptratae (McAlpine et al., 1981).

The Chloropidae is one of the four major families of Diptera that have largely phytophagous larvae (Oldroyd, 1964), being associated particularly with grasses, sedges, and rushes. A few of the plant-feeding forms, such as the frit fly (*Oscinella frit* [L.]) and the wheat stem maggot (*Meromyza americana* Fitch), have become economically important pests of cereals and pasture grasses. In addition to the numerous phytophagous species, there are a fair number of chloropid taxa that have saprophagous larvae and even a few that are predaceous (Oldroyd, 1964; Ferrar, 1987; Sabrosky, 1987). Many of the scavenger species are secondary invaders of plant tissue that has been damaged by the feeding of other insect larvae (Valley et al., 1969). A few species of Chloropidae are of some medical significance. For example, eye gnats of the genus *Liohippelates* (formerly *Hippelates*) are suspected to be vectors of various eye disorders and yaws (Herms, 1928).

Most research on the biology of the family has been restricted to species having agricultural or medical significance, although most chloropids are not thought to be economically important. A few species of *Chlorops, Eribolus, Elachiptera,* and *Oscinella* have been reported to be primary or secondary invaders of stems of wetland monocots belonging to the sedge family Cyperaceae (Valley et al., 1969).

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This paper includes life history data for *Chlorops certimus* Adams and *Epichlorops exilis* (Coquillett), two stem-boring species that attack sedges belonging to the genus *Carex*. The eggs, 3 larval instars, and puparia for both species are described and illustrated.

MATERIALS AND METHODS

Collecting Techniques

Adults were obtained by sweeping herbaceous vegetation in marshy habitats occurring in northeastern Ohio. Captured adults were aspirated alive into 8-dram shell vials and transported to the laboratory where they were placed in breeding chambers. The latter consisted of baby food jars (5 × 7 cm) which had their bottoms removed. A piece of fine mesh nylon was placed over the mouth of the jar and held in place by a rubber band. The open end of the jar was then placed in a petri dish that contained a substrate of moist peat moss. A small pellet of a mixture of honey and brewers' yeast, for adult feeding, was pressed against the upper side of the glass wall. Freshly cut stem sections of potential host plants were placed vertically into the peat moss to provide resting and oviposition sites. Stems were replaced every 2 days. The breeding containers were inspected daily for adult behavior and oviposition.

When eggs were observed, they were carefully removed with a fine camel's hair brush, counted, measured, and placed in small petri dishes containing a piece of moist filter paper. A portion of the leaf blade was also included as substrate. Newly hatched larvae were either set up for life cycle studies or preserved for illustration purposes.

Larval stages were collected in nature by examining potential host plants belonging to the Cyperaceae and other monocot families occurring in the study area. Roots, stems, and inflorescences of suspected host plants were dissected and examined in the field. Immature stages were transferred, along with a portion of the host plant, to an 8-dram shell vial, corked, and held for further investigation. Additional host plants were uprooted, placed in large plastic bags, and taken to the laboratory.

Plants brought back to the laboratory were slit open, and data concerning instar, feeding habits, and position of larvae recorded. Larvae were then transferred to fresh stems and placed in 8-dram shell vials which, in turn, were put into a beaker measuring 9 × 9.5 cm. The beakers (containing as many as six vials) were put into plastic bags (to maintain proper humidity) and placed in a long-day photochamber (16L: 8D) set to promote maximum freshness of the stems (ca. 20°C) without interfering with larval development. Infested stems were checked every 2 days for information concerning feeding habits and duration of larval stadia.

Recently formed puparia were maintained in the sedge culms which were cut into 4 cm lengths and held on moist peat moss in petri dishes. Daily observations provided information on the duration of the prepupal and pupal periods and emergence times of the adults.

Preservation and Preparation of Specimens

Eggs were preserved in ¼ dram vials containing KAAD, plugged with cotton, and stored in 8-dram vials containing 80% ethanol. Larvae were killed either by dropping them in boiling water or by placing them into a stender dish containing KAAD

solution. They were stored in 80% ethanol. Gross morphology was studied by placing eggs and larvae in a small stender dish containing 80% ethanol.

To study minute morphological structures, larvae were dissected with iridectomy scissors, the soft parts being teased away with sharpened minuten pins embedded in the tips of wooden match sticks. Taxonomically important structures (cephalopharyngeal skeletons and anterior and posterior spiracles) were dissected out of the larvae and/or cast exuviae whenever possible. These structures were transferred to microscope slides containing a drop of glycerine and stored in large petri dishes. Occasionally the first and last three segments of the third-instar larvae were dissected away and cleared in hot NaOH or KOH for 5 minutes, after which they were transferred to a depression slide containing a drop of glycerine, and stored in petri dishes.

Puparia were killed in KAAD, measured, and then preserved in 80% ethanol. Puparia that produced adults were placed in #5 gelatin capsules and pinned below the reared adult.

BIOLOGICAL OBSERVATIONS

Chlorops certimus

Chlorops, the largest genus of the subfamily Chloropinae, consists of some 35 species in North America (Sabrosky, 1987). Most species are small and yellow with black or reddish brown mesonotal stripes. Individual species are rarely taken in large numbers and are usually obtained by sweeping wetland herbaceous vegetation.

Most of the life history information for the genus has been restricted to the economically important Palearctic species *Chlorops pumilionis* (Bjerkander). Often called the gout-fly of barley and wheat, this species is responsible for considerable damage to cereal and grain crops throughout Europe (Frew, 1923a, b; Oldroyd, 1964). Its larval stages have been described in great detail by Frew (1923a, b), Goodliffe (1939, 1942), Lilly (1948), Nye (1958), and Dennis (1961).

Larvae of other species of *Chlorops* have also been reported to be primary invaders of grasses and sedges (Wendt, 1968; Zhabinskaya, 1963). *Chlorops obscuricornis* Loew was reared from the spike rush *Eleocharis smallii* Britt. (Valley et al., 1969), and d'Aguilar (1943) reared *C. frontosa* Meigen from the stem of an unidentified species of *Carex.*

Chlorops certimus is a rather common, widely distributed, and highly variable species. It has been recorded from Quebec and Massachusetts west through Ohio, Indiana, and Illinois to Alaska and south to North Carolina, Texas, and Utah (Sabrosky, 1965).

All rearings were initiated from larvae and puparia collected in the culms of *Carex lurida* Wahlenb. or from adults collected in sedge marshes. Larvae of *Chlorops certimus* have also been reported as primary invaders of *Carex hystricina* Muhl. and *C. pennsylvanica* Lam. (Valley et al., 1969).

Adults emerged in nature between late June and late July and remained relatively abundant until mid-August, after which their numbers declined rapidly. The earliest record for captured adults was June 24; the latest, September 29. Males reared from puparia lived 16–21 days; females, 20–33 days. Generally, males emerged first followed in a few days by females.

Field collected and reared adults were kept in rearing chambers along with a portion

of their host plant. In most cases, both sexes remained intimately associated with the provided vegetation, usually resting head downward about one-half to three quarters of the way up the stem. Adults spent very little time on the peat moss, visiting it only to obtain moisture. On many occasions, both males and females were observed grooming themselves on the sides of the rearing chamber and the nylon netting. The front tarsi were used to clean the anterior thoracic and head bristles, and the middle and hind tarsi were repeatedly rubbed over the partially spread wings.

The premating period for laboratory-reared adults was 18–24 hr. On one occasion, a male was seen mating 6–8 hr after emerging with a female that had emerged one day earlier. No overt courtship behavior was noticed. Prior to mating, a male flew to where a female was resting, walked up to her, and when directly in front of her, flew or leaped onto her dorsum. If the female was non-receptive, she immediately decamped by flying or walking away. If the male was aggressive and persisted in his efforts to mount a non-receptive female, she pushed him away by flicking her wings.

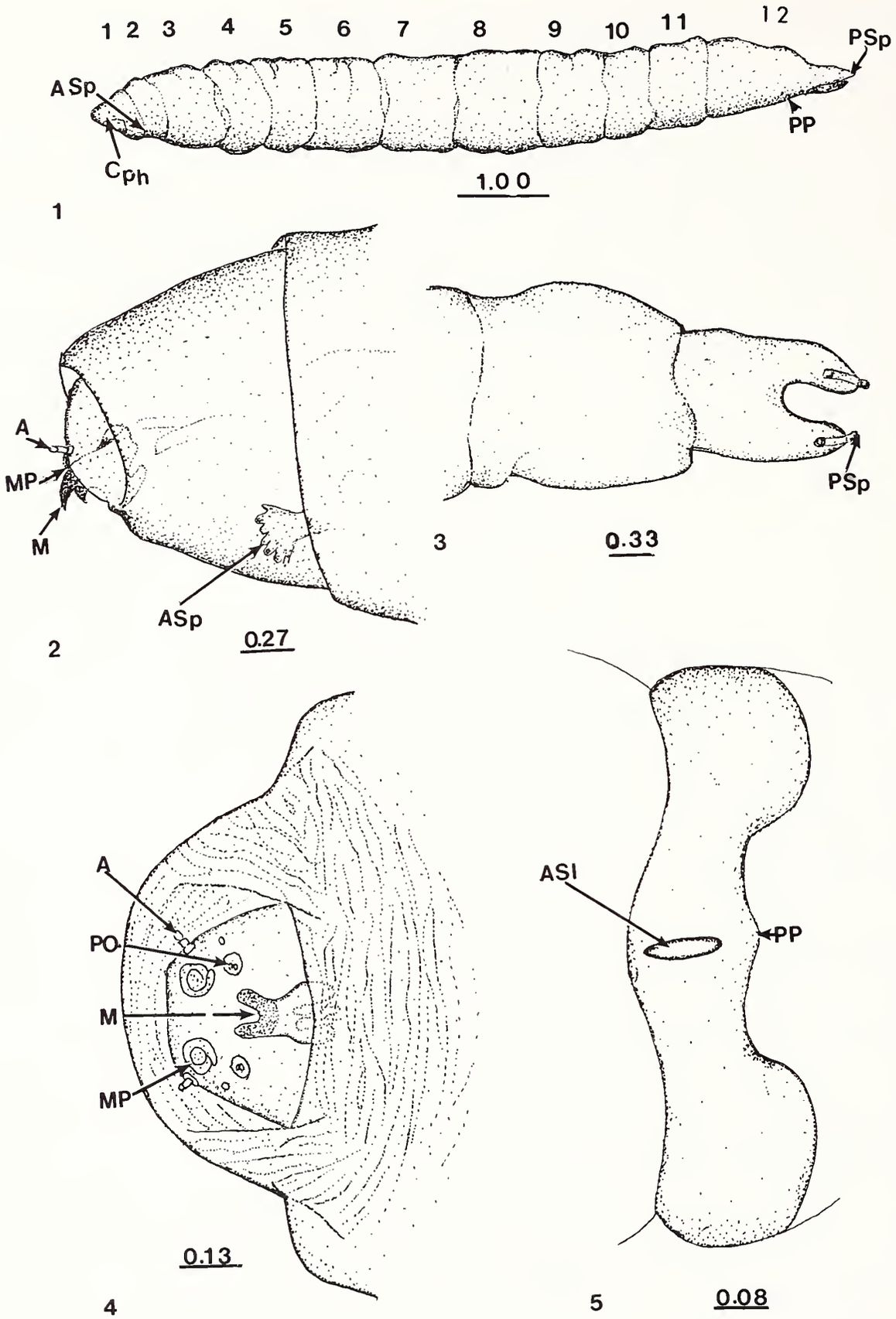
Mating was almost a daily occurrence, and individual pairs often were seen mating as many as three times per day. The average time spent in copula was 35–45 minutes. Mating was observed most frequently during the afternoon and/or early evening hours. Field collected adults usually mated within 10 minutes after being transferred to the plastic rearing chambers.

In copula, the male positioned himself dorsad the female and almost parallel to her body. His head was directly above her scutellum, and his wings were folded flat over his abdomen. The male's fore tarsi were placed on the female's wing bases, and the middle tarsi were appressed against the sides of the female's abdomen approximately one-third of the way back. The hind tarsi of the male were locked around the posterior end of the female's abdomen forming an "X" when viewed from below. The female usually was quite active while in copula. If not walking about the sides of the container, she was usually feeding or grooming her head region with her fore tarsi. At the termination of coitus, the male simply walked off anteriorly.

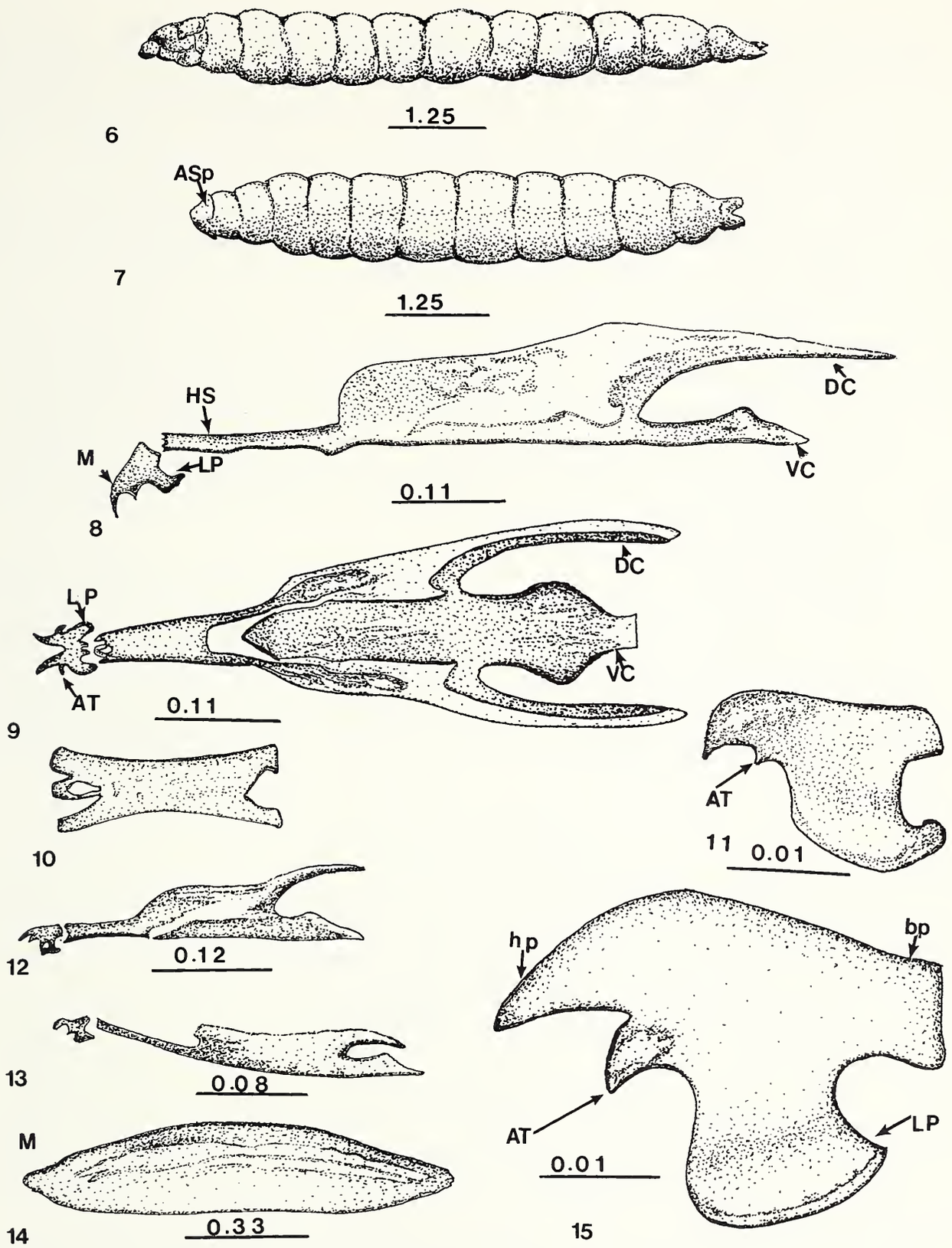
The preoviposition period (from emergence of the female to her first oviposition) lasted 8–14 days. In nature, eggs were found singly on the upper sides of the leaves usually close to the ligule of the host plant. At other times, eggs were found near the tip of the leaf. A few eggs were cemented to the leaf surface between two adjacent longitudinal veins. In the laboratory, field collected and reared females simply deposited eggs on any portion of the vegetation provided as well as on the sides of the rearing chamber and nylon netting.

Two isolated females deposited 65 to 80 eggs, respectively, over a 10–12 day period. The incubation period was 6–7 days. Newly hatched larvae in petri dishes immediately crawled beneath the moist paper toweling. These were transferred to young culms of *Carex lurida* measuring 15–18 cm in height. First instars were very difficult to maintain as they would feed only on fresh stem tissues.

Egg remnants found in nature indicated that newly hatched larvae were oriented with their heads toward the leaf apex. Therefore, larvae must reverse direction and make their way to the ligule and eventually between the overlapping edges of the sheathing leaves. After entering the culm, larvae descended while feeding along the edges of the inner leaves. As larvae moved down the leaf blade, they passed between the successive inner sheaths until they reached the center of the shoot. Repeated observations revealed that larvae bored directly through one or more of the inner



Figs. 1–5. *Epichlorops exilis*, third instar. 1. Lateral habitus. 2. Lateral view of cephalic segment. 3. Dorsal view of posterior end. 4. Ventral view of anterior end showing facial mask. 5. Perianal pad.



Figs. 6–15. *Epichlorops exilis*. 6. Puparium, lateral habitus. 7. Same, dorsal habitus. 8. Third instar, lateral view of cephalopharyngeal skeleton. 9. Same, dorsal view. 10. Same, dorsal view of hypopharyngeal sclerite. 11. Second instar, lateral view of mandible. 12. Same, lateral view of cephalopharyngeal skeleton. 13. First instar, same. 14. Eggs. 15. Third instar, lateral view of mandible.

leaves to reach the center of the culm. Once at the center, the first instars continued to feed as primary invaders on the developing peduncle and tender portions of the innermost leaves. Feeding by the second instars eventually severed the peduncle, thus preventing the inflorescence from growing out of the sheath. The second and third instars then continued to feed on the immature inflorescences and on the peduncle, usually destroying most of the tissues enclosed within the sheath.

In nature, usually one and occasionally two larvae were found per stem. In all cases, they seemingly fed by rupturing individual cells with their highly sclerotized mouthhooks and then sucking up the exuding cellular protoplasm along with structural components of the ruptured cells.

The first larval stadium lasted 24–36 hours; the second, 7 to 10 weeks; and the third, 38–40 weeks. The mature third instar, which usually faced downward, reversed position a short time prior to pupation and migrated a short distance up the stem. Pupation occurred about 1.5 cm below the ligule of the leaf blade. On several occasions, the third instar pupated under the outermost sheathing leaf blades approximately 5–10 cm above ground level. The prepupal period lasted 3–3.5 days; the pupal period, 10–11 days for both sexes.

In northeastern Ohio, *C. certimus* was univoltine, with adults emerging in late June. Eggs were deposited during late June and early July, and larvae became abundant in stands of *Carex lurida* in early to mid-July. Overwintering occurred as larvae in a state of temperature-controlled quiescence; second and third instars collected in November and December began to feed actively when brought into the laboratory, pupated, and eventually emerged as adults. Puparia were encountered in nature between late May and early June.

Epichlorops exilis

The genus *Epichlorops* is represented in North America by only three species. *Epichlorops puncticollis* (Zetterstedt) is Holarctic in distribution, whereas *E. exilis* (Coquillett) and *E. scaber* are strictly Nearctic. The taxonomy of the genus is relatively well understood, but information on the biology and immature stages is lacking.

Morphologically, the genus *Epichlorops* appears to be closely allied to the genera *Chlorops* Meigen and *Cetema* Hendel (Becker, 1910). However, adults of *Epichlorops* are easily recognized in that they are conspicuously large and have a characteristically yellow and black body. In addition, the dorsum of the thorax is uniformly black, without the longitudinal stripes that are characteristic of *Chlorops.* Also in contrast to *Chlorops,* the dorsum of the thorax is strongly punctate, a condition similar to that found in *Cetema.*

Epichlorops exilis is an attractive, moderately large fly measuring 4–5 mm in length. Adults are easily recognized by the yellow head that bears a conspicuously shiny black ocellar triangle, the black abdomen with the sides and venter yellow, the uniformly black body and coarsely punctured mesonotum, and by the yellow scutellum. The species ranges from Massachusetts to Washington and Saskatchewan, and south to Ohio and Iowa (Sabrosky, 1965).

Biological observations are based on rearings initiated from larvae and puparia found in stems of *Carex crinita* Lam. and from adults collected in sedge marshes.

Adults were abundant in moist, partially shaded regions of marshes, particularly

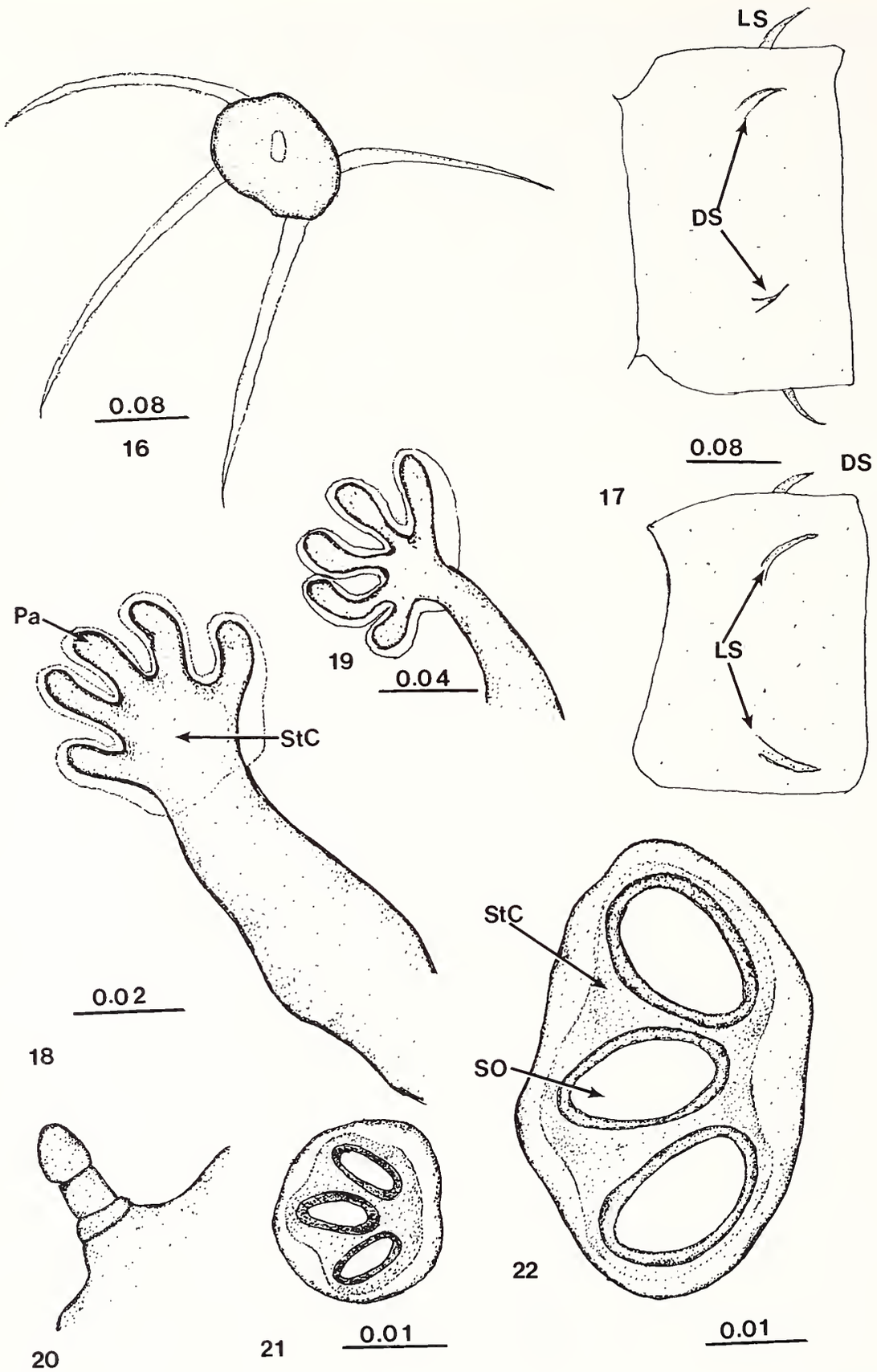
in the early morning hours. They showed fidelity to their host plants, and only a few specimens were taken in adjacent stands of wetland monocots. In a marsh near Kent, adults were abundant in a stand of *Carex lacustris* Willd.; occasional in reed canary grass, *Phalaris arundinacea* L. (a few plants of *C. lacutris* occurred in this stand); and very rare in *Carex stricta* Lam. (Fig. 42). Both males and females were often observed resting on stems with their heads facing downwards. They were usually seen about three quarters of the way up the stems of their host plant, or horizontally on the dorsal surfaces of the leaf blades near the ligule of the culm. On several early morning collecting trips, males and females were often observed extending and retracting their proboscis into and out of drops of dew that had collected the night before on the leaf blades and stems.

In the laboratory, adults of *E. exilis* were confined to rearing chambers and provided with a portion of a stem of *C. crinita* measuring 10 cm in length. Both sexes spent much time on the stems, usually walking up and down the sheathing leaves. On several occasions females were observed near the ligule of the stem, oriented towards the apical end of the leaf blades. This is the normal ovipositing position. When not ovipositing, they were observed grooming themselves with their front tarsi. When on the sides of the jar, they appeared to walk side ways. They always remained in close proximity to each other. However, if surprised or frightened by sudden movement of the light or jarring of the table, both sexes quickly retired to the vegetation or peat moss. Frequently they were seen mating while upside down on the cloth netting that covered the mouth of the breeding jar.

Gravid females collected in nature lived from 10–14 days in the laboratory; males, 10–12 days. If reared from larvae or puparia, males lived from 25–30 days; females, from 29–30 days. Sexual dimorphism was evident, as females were distinctly larger.

In the laboratory adults were frequently observed feeding on the fly food. In most cases, water was obtained from droplets that collected on the vegetation from daily watering or from the moistened peat moss. If the peat moss was too moist, adults frequently became trapped and were often found dead the next morning. Grooming activity usually centered about the head and wings. The front tarsi were used to clean the head bristles and antennal regions, and the middle tarsi were used to groom the wings and mid-section of the abdomen. The posterior part of the abdomen was cleaned with the last pair of tarsi.

Mating was observed in nature commonly in the early morning hours, usually between 8:30 and 10:30 AM, and in the evening. In the laboratory, mating occurred repeatedly with no obvious preference as to time of day. In general, mating took place shortly after adult emergence. The premating period averaged between 16 and 24 hours, the time probably required for partial sclerotization of the exoskeleton and complete body pigmentation. No overt courtship behavior was observed, although the male periodically was seen presenting himself to the female by walking up to and then standing directly in front of her. Non-receptive females would turn around and walk away or fly to the side of the rearing chamber. If a male attempted to mount a non-receptive female, she would dislodge him by simply flicking her wings. A receptive female remained relatively motionless for a moment and then, after a short period of grooming, extended her wings laterally away from her body (about 40–45°). The male then either walked around her and mounted posteriorly or simply flew onto her back. Both procedures were observed on several occasions.



Figs. 16–22. *Epichlorops exilis*. 16. First instar, posterior spiracular plate. 17 (top). Same, dorsal view of fifth abdominal segment showing spines. 17 (bottom). Same, lateral view. 18. Third instar, anterior spiracle. 19. Second instar, same. 20. Third instar, antenna. 21. Second instar, posterior spiracular plate. 22. Third instar, same.

Females mated several times with either the same male or with other males. According to Gilbertson (1925), sunlight apparently acts as a stimulus to bring about mating in species of Chloropidae, at least in *Meromyza americana* Fitch. No male guarding of recently mated females was observed.

During copulation, the male positioned himself above the female with his head directly over the posterior part of her scutellum. He was positioned at about a 40° angle to the larger female, with the terminal end of his abdomen strongly curved downwards to meet the female's genitalia. His wings were folded; the female's wings were spread laterally at about a 45° angle from her body. The male's foretarsi were placed on the wing bases of the female, although they were seen occasionally to grasp her costal vein near the wing bases. His middle tarsi were tightly appressed against the middle of the female's abdomen, about two-thirds of the way back, and his hind tarsi either grasped the copulatory organs of the female or manipulated her genitalia. On several occasions the male extended his proboscis and touched the female's scutellum. During mating both sexes frequently had the wings folded over their abdomens, with the apical portion of the female's wings being bent downward. However, in most cases, the mating position consisted of the female extending her wings laterally away from her body. Adults usually remained in coitus for 45–65 minutes, although one copulation lasted nearly 2.5 hours.

The preoviposition period lasted between 8 to 12 days ($\bar{x}$ = 9, N = 10). Females collected in nature as well as those reared in the laboratory readily oviposited in the breeding jars. In nature, eggs usually were found on the upper surface of the leaves of the host plant close to the culm. They were also found on the stem close to a leaf sheath or between the sheath and the stem. In contrast, females held in breeding jars showed no obvious preference for a particular oviposition site and scattered their eggs over all parts of the host plant as well as on the sides and netting of the container. However, no eggs were found on the moist peat moss substrate. Eggs that had been deposited on leaves of the host plant usually were so oriented that their longitudinal axes were parallel to the veins of the leaf.

During oviposition, the last three abdominal segments were extended to form a telescopic tube. The female used this structure to probe the surface of the host plant for a few seconds before depositing an egg. Each oviposition required only a few seconds, with eggs being attached to the substrate by a glue-like material. In nature, eggs of *E. exilis* were deposited singly, with only 1 or 2 per host plant.

Four laboratory-reared females deposited 40, 48, 50, and 55 eggs, respectively, over a 10 to 12 day period. An average of 5 eggs per female was deposited daily. The incubation period lasted 8–10 days. Shortly before hatching, the mouthhooks of the larvae rubbed against the inner surface of the egg. Typically, larvae required 30–35 minutes to escape the egg membranes.

A newly hatched larva crawled down into or around the ligule of the culm until it reached the slit in the overlapping sheathing portion of the leaves. After entering the space between the leaves, the larva continued to move downwards along the edges of the leaves until it reached the soft succulent tissues at the base of the stem. Minute feeding trails were formed during this initial movement downward. Once at the stem base, the larva penetrated the successive layers by cutting inwards and downwards in a spiral manner until it reached the center of the shoot. Most of the feeding by the second and third instars occurred at the base of the stem, with most

of the tissue near the center of the culm being destroyed. Larvae were found in nature in culms of *C. crinita, C. lacustris,* and *C. lurida* Wahlenb., but not in *C. stricta.*

Larvae apparently rasped the plant tissues with their mandibles, causing cells to rupture and exude sap. The plant juices and the damaged tissues were then ingested. Areas being fed upon quickly became filled with decomposing plant tissue and fecal material that formed conspicuous feeding trails within the stems. Infested plants were easily recognized by the presence of these feeding trails. Plants that were in flower were rarely attacked, possibly because the stem tissues had become tough and fibrous.

The first larval stadium lasted 24–36 hours; the second, 1–2 weeks; and the third, 40–52 weeks. After overwintering, a mature larva reversed direction in the stem and moved upwards between the ensheathing leaves. It then defecated before forming a puparium about 2.5 cm below the ligule of the leaf sheath. The prepupal period lasted 2–3 days; the pupal period, 10–11 days for males (N = 12) and 12–14 days for females (N = 10).

Epichlorops exilis was an univoltine species in northern Ohio. Adults emerged in nature between mid-May and early June. Adult populations remained quite high until mid-June but then declined dramatically (Fig. 43). The earliest collection date for an adult was May 16; the latest, June 30. Overwintering occurred as nearly mature larvae in a state of temperature-induced quiescence, usually below ground level, at the base of the stem of the host plant. Larvae that had overwintered were observed to feed for a few days in early April before migrating upwards in the culm during early May to form puparia.

DESCRIPTIONS OF IMMATURE STAGES

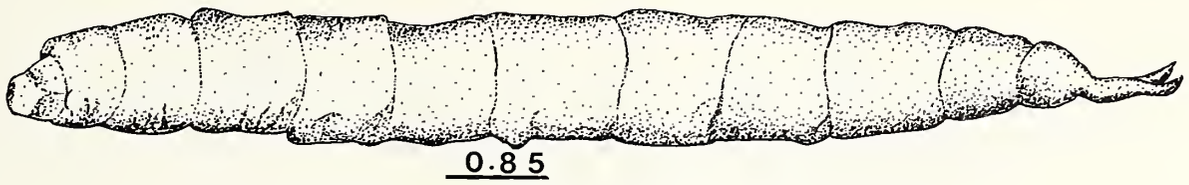
Chlorops certimus

Egg (Fig. 34): Length 0.89–0.93 mm, maximum width 0.18–0.19 mm. Slightly flattened dorsoventrally, tapering anteriorly with micropylar end smaller than rounded posterior end. Ventral surface slightly flattened. Chorion with thin ridges anastomosing and forming delicate reticulations. Areas between ridges with indistinct bead-like pattern.

First instar larva: Similar to third instar except in following characters. Length 0.91–1.64 mm, greatest width 0.15–0.27 mm. Cylindrical to conical. Posterior fleshy projection (Fig. 36) smaller, with 2 short, stout spines distally. Stigmatic chamber and clear areas (Fig. 37) indistinct, only distal spines (reduced spiracular hairs) conspicuous. Thoracic and abdominal segments each with 2 dorsal and 2 lateral spines. Larva metapneustic. Cephalopharyngeal skeleton (Fig. 35) length 0.16–0.18 mm, greatest width 0.02–0.03 mm; lightly pigmented; dorsal and ventral cornua hyaline; hypopharygeal sclerite with 1 clear window.

Second instar larva: Similar to third instar except in following characters. Length 1.69–2.68 mm, greatest width 0.21–0.34 mm. Anterior spiracles (Fig. 41) smaller, inconspicuous, with 3–4 marginal papillae. Cephalopharyngeal skeleton (Fig. 33) length 0.36–0.39 mm, greatest width 0.08–0.09 mm.

Third instar larva (Fig. 23): Length 6.69–8.13 mm, greatest width 0.79–1.15 mm. Creamy white to opaque, integument transparent to translucent, spinulose and shiny. Body elongate, somewhat flattened dorsoventrally, tapering slightly anteriorly; amphipneustic. Posterior end bilobed and terminating in 2 slightly elongate, barrel-



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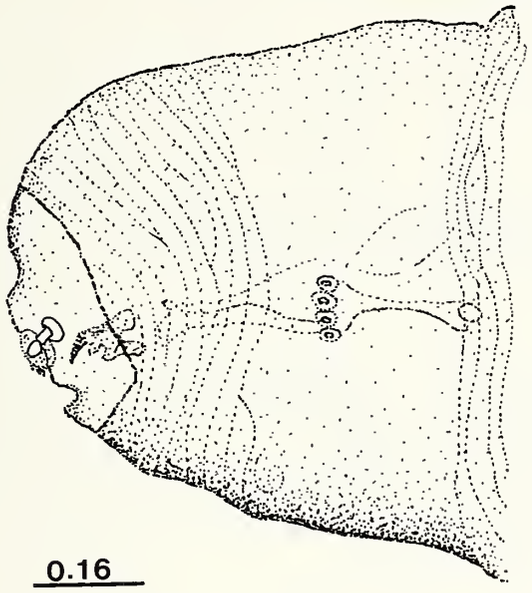

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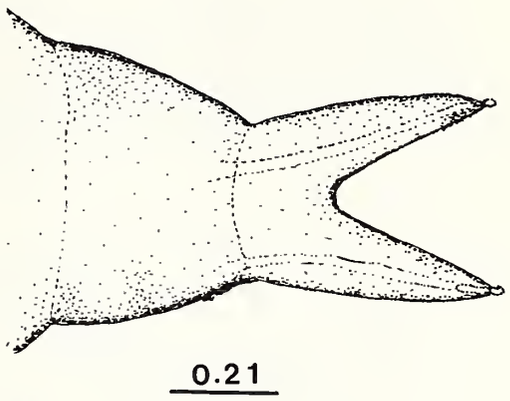

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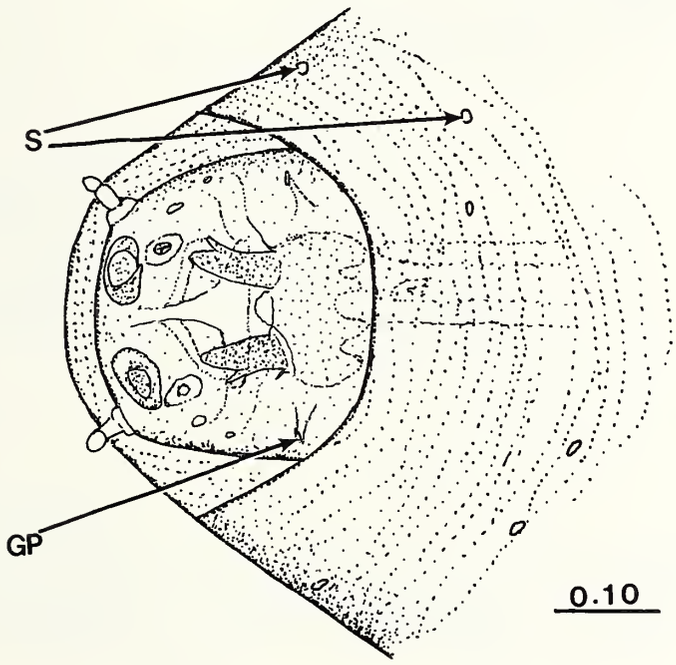

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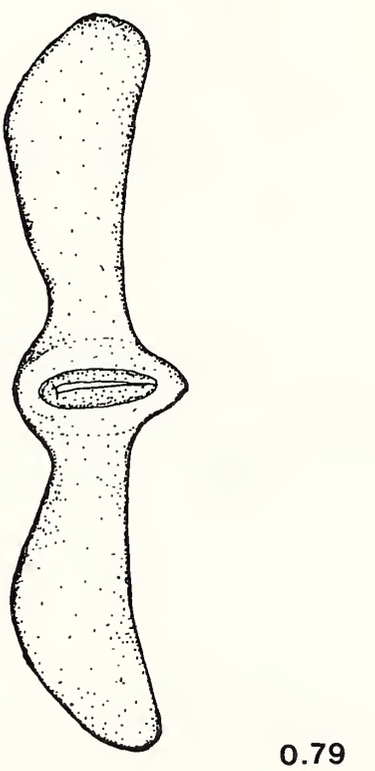

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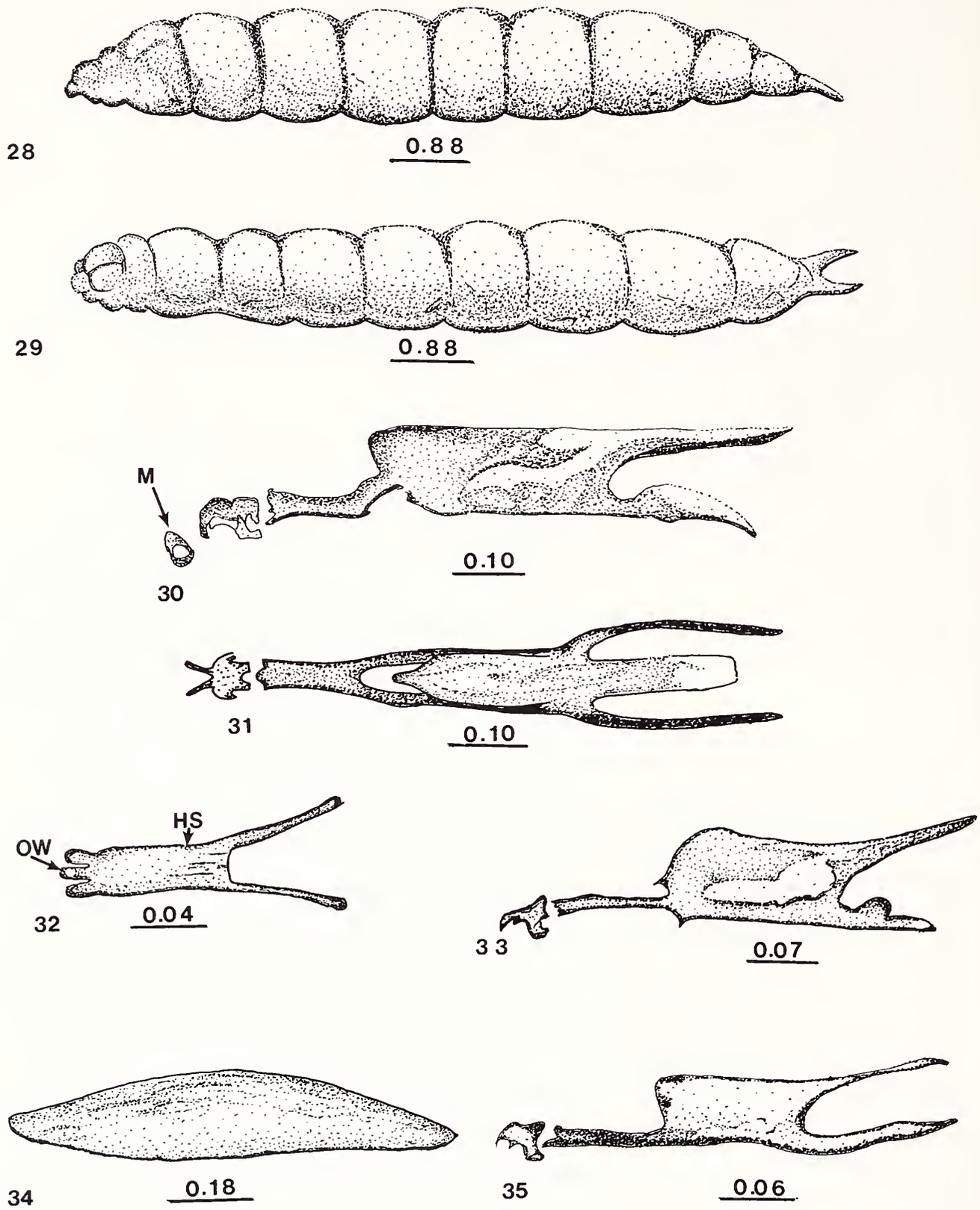
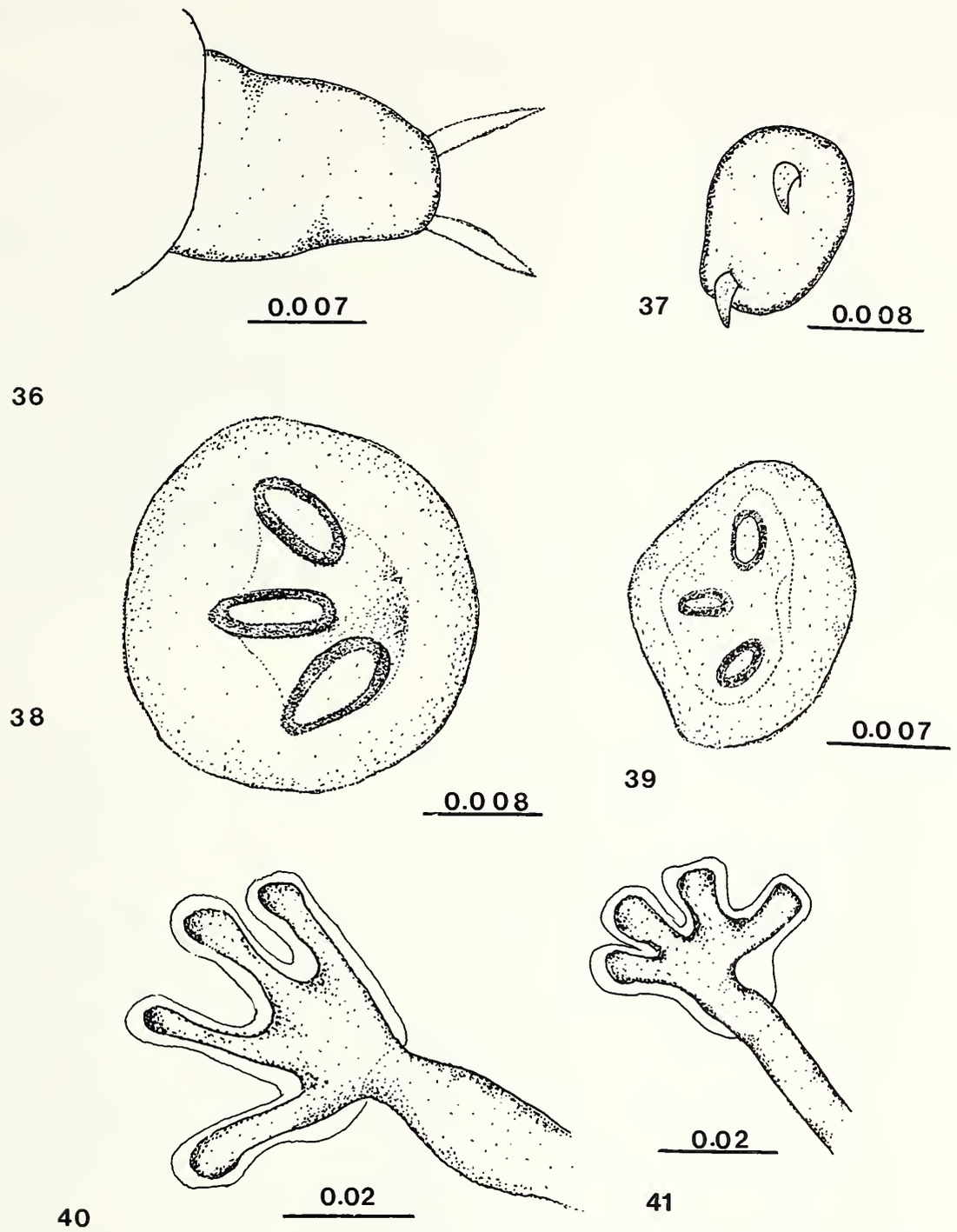
Figs. 23–27. *Chlorops certimus,* third instar. 23. Lateral habitus. 24. Lateral view of anterior end. 25. Dorsal view of posterior segment. 26. Ventral view of anterior end showing facial mask. 27. Perianal pad.

shaped spiracular tubes. Segment 1 (cephalic) (Figs. 24, 26) highly retractile, bilobed anteriorly; each lobe bearing short fleshy, 3-segmented antenna, maxillary palp with 6–8 sensory pegs, and genal palp with 1 sensory peg; oral ridges bordering mouth opening not bifurcating. Segment 2 (prothoracic) with 30–35 irregular rows of v-shaped



Figs. 28–35. *Chlorops certimus.* 28. Puparium, lateral habitus. 29. Same, dorsal habitus. 30. Third instar, lateral view of cephalopharyngeal skeleton. 31. Same, dorsal view. 32. Same, dorsal view of hypopharyngeal sclerite. 33. Second instar, lateral view of cephalopharyngeal skeleton. 34. Egg. 35. First instar, lateral view of cephalopharyngeal skeleton.



Figs. 36–41. *Chlorops certimus*. 36. First instar, dorsal view of posterior end. 37. Same, posterior spiracular plate. 38. Third instar, same. 39. Second instar, same. 40. Third instar, anterior spiracle. 41. Second instar, same.

spinules encircling segment; with 6 sensory sensilla on ventral surface, each sensillum surrounded by thick triangular spinules. Segments 3–12 with 15–20 small, reduced spinule rows, these becoming indistinct fine lines anteriorly, only 5–10 rows encircling anterior portion of each segment. Primary integumentary folds between abdominal segments with 25–35 or more rows of reduced spinules. Posterior segment (Fig. 25) tapered and terminating in 2 elongate, somewhat triangular fleshy projections. Perianal pad (Fig. 27) bilobed, with anal slit medially, no spinule patch near pad.

Anterior spiracles (Fig. 40) fan-shaped, with 4 apical papillae, each papilla surrounded by transparent membrane.

Posterior spiracles distally at apices of 2 fleshy projections. Spiracular plates indistinct (Fig. 38), with 3 spiracular openings but no spiracular hairs.

Cephalopharyngeal skeleton (Figs. 30, 31) length 0.58–0.61 mm, greatest width 0.11–0.13 mm; heavily pigmented except for light areas on posterior ends of cornua; hypopharyngeal sclerite (Fig. 32) H-shaped, fused with lightly pigmented tentoropharyngeal sclerite; hypopharyngeal plate extending anteroventrally, with anterior oval window and 4 smaller lateral windows; dorsal cornua not connected anterodorsally; floor of tentoropharyngeal sclerite lacking pharnygeal ridges, sclerite lightly pigmented; mandibles fused posterodorsally, deeply pigmented except on accessory teeth and lateral processes; hook part strongly decurved, with sharp accessory tooth.

Puparium (Figs. 28, 29): Elongate with both ends flattened dorsoventrally, segments 1–4 with noticeable lateral ridges. Cuticle thin and transparent, with contained pupa visible; spinule pattern that of mature larva. Length 7.68–7.71 mm, greatest width 1.78–1.80 mm. Anterior spiracles anterolaterad on first apparent segment, with 4 inconspicuous apical papillae. Posterior spiracular tubes elongate, abruptly tapered, and somewhat triangular. Posterior spiracular plates indistinct, and slightly turned upward. Perianal pad as in mature larva.

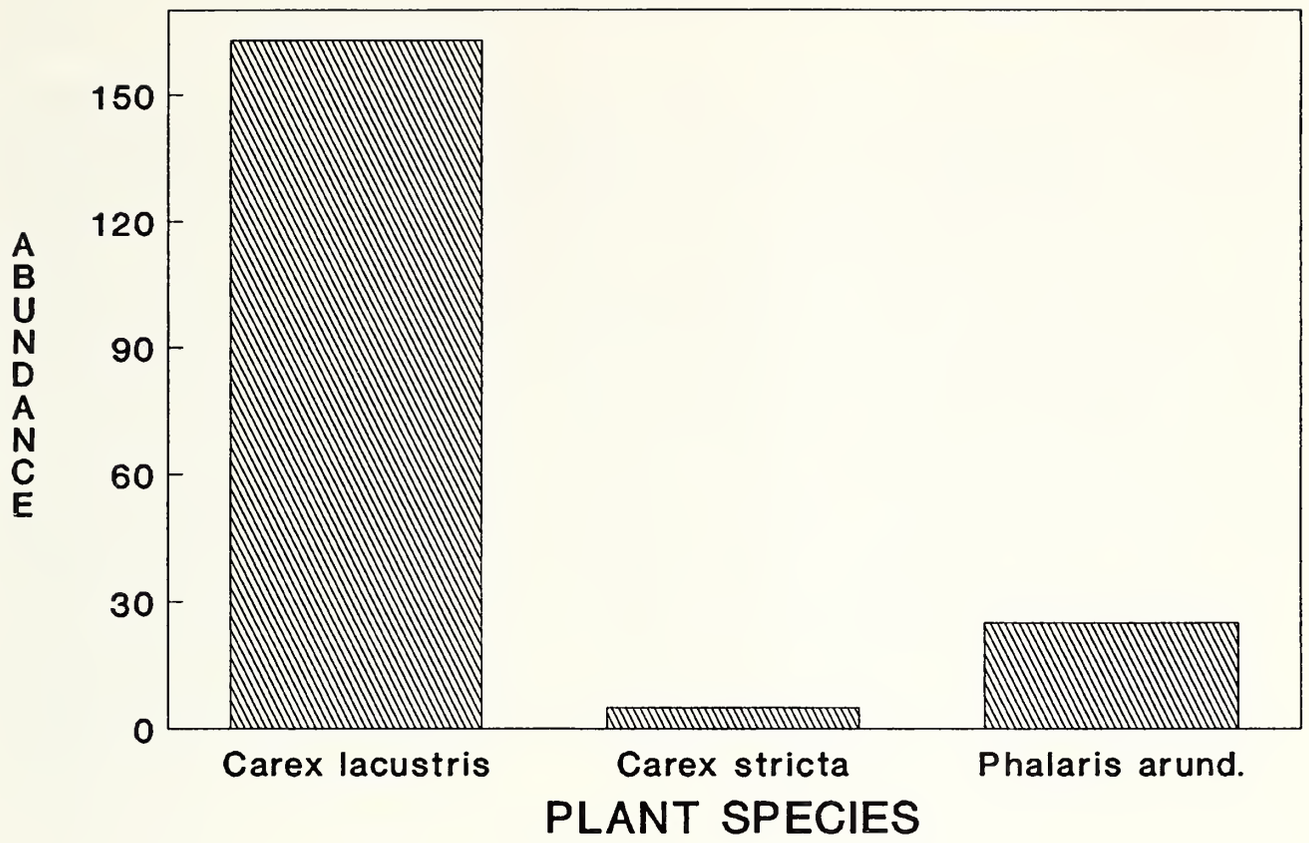
Epichlorops exilis

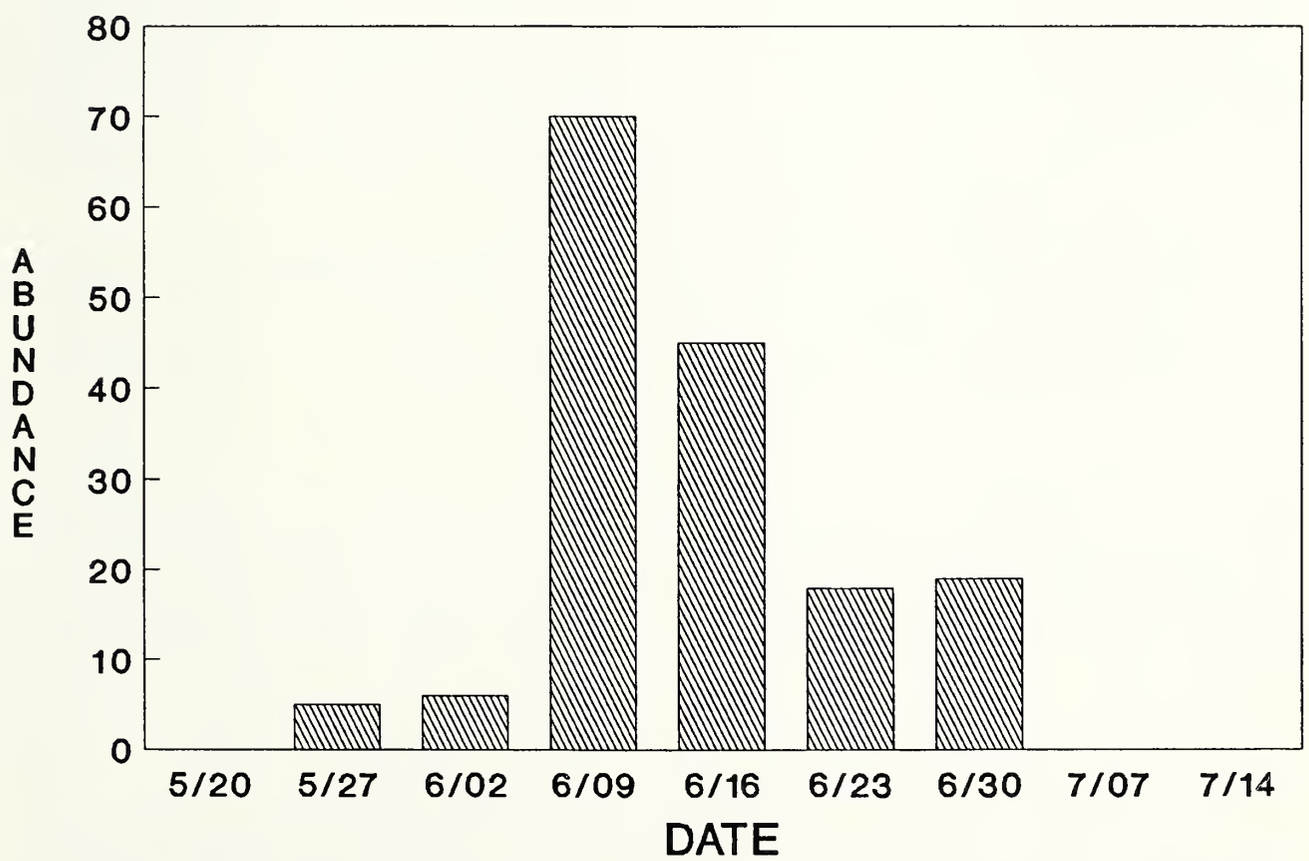
Egg (Fig. 14): Length 1.35–1.70 mm, greatest width 0.19–0.21 mm. White to semitransparent, slightly flattened dorsoventrally. Micropylar end tapering and slightly smaller than rounded posterior end, micropyle facing downward. Ventral surface somewhat flattened, opaque to translucent, not ridged, and lacking fine reticulation. Chorion otherwise with fine polygonal reticulation pattern.

First instar larva: Similar to third instar except in the following characters. Length 1.80–1.95 mm, greatest width 0.12–0.21 mm. Pale white to translucent, integument spinulose. Body conical to cylindrical. Posterior spiracular plates indistinct, at apices of short spiracular tubes; plates (Fig. 16) with 4 elongate, thin, spiracular hairs; spiracular clear areas indistinct. Larva metapneustic. Segments 2–11 each with 2 lateral and 2 dorsal spines (Fig. 17 top, bottom) all projecting posteriorly. Segment 12 with dense dorsoventral spinule patch with 10–15 rows completely encircling segment. Cephalopharyngeal skeleton (Fig. 13) length 0.28–0.30 mm, greatest width 0.04–0.05 mm; tentoropharyngeal sclerite lightly pigmented, fused with hypopharyngeal sclerite; latter sclerite projecting under posteroventral portions of mandibles; mandibles paired, slightly pigmented and fused posterodorsally; hook part, accessory tooth and lateral process lightly pigmented. Accessory tooth arising from side in lateral view.

Second instar larva: Similar to third instar except in the following characters. Length 2.45–2.85 mm, greatest width 0.61–0.71 mm. Pale white to transparent, integument spinulose. Posterior spiracular plate (Fig. 21) smaller, slightly circular to oval, without spiracular hairs. Anterior spiracles (Fig. 19) short and inconspicuous, lightly pigmented, with 5 marginal papillae; each papilla surrounded by transparent membrane. Cephalopharyngeal skeleton (Fig. 12) length 0.47–0.50 mm, greatest width 0.06–0.08 mm. Faintly to moderately pigmented; cornua hyaline; paired mandibles (Fig. 11) fused and heavily pigmented dorsoposteriorly; hook part, accessory tooth, and lateral process lightly pigmented.

Third instar larva (Fig. 1): Similar to that of *C. certimus* except in following characters. Length 7.92–9.37 mm, maximum width 1.52–1.54 mm from thoracic





Figs. 42–43. *Epichlorops exilis.* 42. Distribution of adults in three stands of marsh monocots near Kent, Ohio. 43. Seasonal distribution of adults in stand of *Carex lacustris* near Kent, Ohio.

segment 3; amphipneustic. Segment 1 (Figs. 2, 4) with base of antenna platelike (Fig. 20); maxillary palp consisting of laterally thickened, pigmented ring encircling 5–6 sensory pegs; preoral palp just below maxillary palps consisting of 2 sensory pegs; each lobe also bearing lateral papilla and sharing medioventral, circular to lightly oval sensory plate with 2 sensory papillae; oral ridges not bifurcating, directed towards oral opening. Segment 2 (Fig. 2) bearing anterior spiracles posterolaterally. Perianal pad (Fig. 5) as in *C. certimus.* Anterior spiracles (Fig. 18) conspicuous, fan-shaped, bearing 5–6 apical papillae. Each papilla slightly pigmented, and surrounded by transparent membrane. Posterior spiracles (Fig. 3) similar to those of *C. certimus.*

Cephalopharyngeal skeleton (Figs. 8, 9) length 0.74–0.80 mm, greatest width 0.13–0.16 mm; hypopharyngeal sclerite (Fig. 10) with hypopharyngeal plate with clear oval window, middle of plate heavily pigmented with 2 small clear windows and two lateral notches; mandibles (Fig. 15) very similar to those of *C. certimus.*

Puparium: Very similar to that of *C. certimus* except in following characters. Length 9.00–9.16 mm, greatest width 0.89–0.92 mm. Anterior spiracles with 5–6 apical papillae. Posterior spiracular plates deeply pigmented, rounded, and slightly turned upward; spiracular openings distinct.

DISCUSSION

Although the larval feeding habits of only 15–20% of the Nearctic Chloropidae are known, several species have been found to have saprophagous larvae (Valley et al., 1969). This suggests that the ancestral Chloropidae were also scavengers. This is in agreement with Oldroyd (1964), who speculated that all modern groups of Diptera evolved from compost-feeding ancestors. If so, the precursors of such present-day primary invaders as the species of *Chlorops* and *Epichlorops* may be best typified by the rather generalized way of life found in the genus *Elachiptera.* Larvae of this genus develop equally well on leaf mold, rotting vegetation, and decaying wood (Oldroyd, 1964). Possibly, the evolutionary pathway leading to phytophagy was from scavenging on decaying plant material to being a secondary invader of plant tissues damaged by some primary invader to being truly phytophagious.

Seemingly unique (apomorphic?) for the phytophagous Chloropinae are the fleshy lobes (stigmatophores) that project posteriorly from the caudal segment (Fig. 3). Nowicki (1873) was the first to note these lobes and suggested that they were taxonomically significant. Similar lobes have not been found in any of the secondary invaders that have been investigated. Wearsch (1968) described them in larvae of *Diplotoxa,* which feed as primary invaders in stems and rhizomes of spike-rush (*Eleocharis* spp.). Mature larvae of *Diplotoxa* are easily distinguished from those of *Epichlorops* and *Chlorops* in that they all possess 3–4 branching spiracular hairs, whereas larvae of *Epichlorops* and *Chlorops* lack such hairs. The fleshy lobes vary in size, shape, and pigmentation and could prove useful in differentiating closely related species.

The cephalopharyngeal skeletons of *C. certimus* and *E. exilis* larvae are very similar (Figs. 8, 30). Mandibles of the third instar larva (Fig. 15) typically consist of a large, heavily sclerotized apical hookpart, a lightly pigmented accessory tooth, and a moderately pigmented lateral process. The mandibles rasp and cut through the plant tissues, enabling larvae to feed on the exuding cellular protoplasm. Perhaps the most interesting speculation about the cephalopharnygeal skeleton concerns the lateral

processes that project from the posterolateral portions of the mandibles (Fig. 15). These slightly upward-curving projections appear to be characteristic of *Chlorops* and *Epichlorops*. Judging from the illustrations of Valley (1968), the lateral processes may have evolved from the fusion of the dental sclerites with the mandibles. Originally, the dental sclerites probably were very similar to those found today in *Lasiosina canadensis* Aldrich (Valley, 1968). The position of the dental sclerites and their degree of fusion with the mandibles appear to reflect the feeding habits of the larvae. In *L. canadensis,* a secondary invader, the dental sclerites are closely associated with the mandibles but not fused to them. Possibly they provide areas for muscle attachment that help coordinate movements of the mandible. In *Meromyza americana,* a primary invader of grasses, the dental sclerites (as illustrated by Allen and Painter, 1937) are larger, slightly arched, and partially fused to the mandibles. In *Epichlorops* and *Chlorops,* which have somewhat similar feeding habits, there are no obvious dental sclerites. However, the lateral processes are well developed and very similar morphologically to the partially fused dental sclerites shown in *M. americana.* This suggests that in *Chlorops* and *Epichlorops* the dental sclerites have become solidly fused to the mandibles.

The shape of the tentoropharyngeal sclerite of *Epichlorops* and *Chlorops* also appears to reflect the larval feeding habits. Unlike those of such secondary invaders as *L. canadensis* and *Elachiptera costata* (Loew), larvae of the primary invaders lack longitudinal ridges in the floor of the pharnyx. Pharyngeal ridges have been reported in scavenging larvae of Otitidae, Lauxiniidae, Ephydridae, and several other families of muscomorphous Diptera. Presence or absence of the pharnygeal ridges may reflect the nutritional value of the liquid portions of the food substrate. According to Dowding (1987), pharnygeal ridges function as a sieve that filters out and concentrates small food particles from a semiliquid substrate. The ridges, therefore, are advantageous to scavenging larvae that are essentially particle feeders. However, larvae of *Epichlorops* and *Chlorops* utilize highly nutritious protoplasm, and there would be no selective advantage in retaining pharyngeal ridges.

The mature larvae of *C. certimus* and *E. exilis* are very similar, and the two species cannot be readily distinguished. The anterior spiracles of *C. certimus* possess only 4 marginal papillae, whereas those of *E. exilis* have 5–6 papillae. In contrast, the first instars of *E. exilis* are easily distinguished from those of *C. certimus* by the presence of four elongate, non-branching spiracular hairs in the former species (Fig. 16).

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EXPLANATION OF LABELS ON FIGURES

A, antenna; ASl, anal slit; ASp, anterior spiracle (m, membrane); AT, accessory tooth; Cph, cephalopharyngeal skeleton; DC, dorsal cornu; DS, dorsal spine; GP, genal papilla; HS, hypopharyngeal sclerite; LP, lateral process; LS, lateral spine; M, mandible (bp, basal part, hp,

hook part); MP, maxillary palp; OW, oval window; Pa, papilla; PO, preoral palp; PP, perianal pad; PSp, posterior spiracle; S, sensilla; StC, stigmatic chamber; SO, spiracular opening; TS, tentoropharyngeal sclerite; VC, ventral cornu.

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